Effects of Photoperiod on Boll Weevil (Coleoptera: Curculionidae) Development, Survival, and Reproduction

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ABSTRACT Effects of photoperiod on development, survival, feeding, and oviposition of boll weevils, *Anthonomus grandis grandis* Boheman, were assessed under five different photophases (24, 14, 12, 10, and 0 h) at a constant 27°C temperature and 65% RH in the laboratory. Analyses of our results detected positive relationships between photoperiod and puncturing (mean numbers of oviposition and feeding punctures per day), and oviposition (oviposition punctures/oviposition+feeding punctures) activities, and the proportion of squares attacked by boll weevil females. When boll weevil females developed in light:darkness cycles, they produced a significantly higher percentage of eggs developing to adulthood than those developed in 24-h light or dark conditions. In long photoperiod (24:0 and 14:10 h), the number of female progeny was significantly higher and their development time was significantly shorter than those developed in short photoperiod (0:24 and 10:14 h). Lifetime oviposition was significantly highest at 12- and 14-h photophase, lowest at 0- and 10-h photophase, and intermediate at 24 h of light. Life table calculations indicated that boll weevil populations developed in a photoperiod of 14:10 and 12:12 (L:D) h will increase an average of two-fold each generation (R_o) compared with boll weevils developed in 24:0- and 10:14-h photoperiods and 15-fold compared with those at 0:24 h. Knowledge of the photoperiod-dependent population growth potential is critical for understanding population dynamics to better develop sampling protocols and timing insecticide applications.

KEY WORDS *Anthonomus grandis grandis*, boll weevil, cotton, photoperiod

The seasonal activity of many insects is governed by abiotic factors, and light is the basic factor that determines timing of organism activity in most cases. Along with temperature, the daily cycle of light and darkness is one of the main environmental factors affecting population phenology and density of insects during the growing season and timing of life history events (Luker et al. 2002). Reproductive tactics of some insects are also affected by photoperiod because daylength is a reliable cue indicating seasonal changes in environmental suitability (Luker et al. 2002). The boll weevil, *Anthonomus grandis grandis* Boheman, has been a major pest of cotton in the United States since its invasion from Mexico beginning in 1892 (Burke et al. 1986, Hunter and Coad 1923). As with many tropical insects

(Denlinger 1986), it undergoes an adult diapause or quiescence originally related to tropical wet and dry season, or host availability associated with those seasons, which preadapted it to overwintering in temperate zones after invasion. Although it has been long assumed that photoperiod induces boll weevil adult diapause (Brazzel and Newsom 1959, Mangum et al. 1968, Wagner et al. 1999), it is now clear that adult diet controls dormancy induction and that photoperiod plays little, if any, role (Lloyd et al. 1967, Spurgeon and Raulston 1998, 2006, Lewis et al. 2002).

However, many other aspects of an insect's life cycle, including feeding rate, fecundity, survival, and development rate (Umble and Fisher 2002, Berkvens et al. 2006, Omkar and Pathak 2006), are frequently affected by photoperiod. Such effects can be an artifact of more or less hours of daylight available for feeding but are often the result of hormonal responses to daylength (Whittaker and Kirk 2004). Understanding these effects is important to predicting population growth at different latitudes and seasons. Little is known about the effects of photoperiod on life history traits of the boll weevil.

The aim of this study was to determine the effects of photoperiod on boll weevil feeding, fecundity, survival, development, and sex ratio in laboratory tests.

Materials and Methods

Boll Weevil and Cotton Squares. To help avoid potentially confounding effects of developmental history on our results, we reared all experimental insects in the laboratory. Adult boll weevils were obtained from larval-infested cotton squares collected in the Lower Rio Grande Valley of Texas in the 2004 and 2005 cotton growing seasons. Squares were carefully dissected to confirm infestation, and those with live third instars were reclosed and held in screened cages in an environmental chamber at $27 \pm 1°C$, 65% RH, and a photoperiod of 13:11 (L:D) h. Temperature and humidity were monitored by a Fisher brand traceable relative humidity meter with temperature readout (catalog no. 11-661-12; Control Company, Friendswood, TX). When $\approx 60\%$ of boll weevil larvae had pupated, the pupae were harvested from squares and placed in 9-cm-diameter petri dishes (10 per petri dish) containing a thin layer of moist vermiculite. Pupae were examined daily until adult eclosion. On the day of eclosion, adults were sexed using the method of Sappington and Spurgeon (2000) and weighed on an analytical balance. Males were marked with a red paint pen (Painters Medium; Hunt, Statesville, NC) on the right elytron. Only adults weighing between 10 and 15 mg on the day of eclosion were used in the study. To ensure mating occurred, groups of 20 boll weevils (10 males and 10 females) were kept together in petri dishes with a 4-cm-diameter circular screened hole (organdy cloth) in the lid for ventilation for 120 h under the same environmental conditions used for rearing larvae. Each dish contained a cotton wick saturated with distilled water and was provided daily with uninfested, greenhouse-grown cotton squares (7–10 mm in diameter at the widest part of the flower bud) with intact bracts.

Experimental Conditions. Five photoperiods were used: 10:14; 12:12; 14:10; 24:0; and 0:24 (L:D) h. Photophase was initiated at 0700 hours. In all cases, temperature was maintained at $27 \pm 1°C$ and humidity at 65%. Groups of 10 females were conditioned to their assigned photoperiod for 5 d before studies. There were 10 replications (females) per treatment. Each female was isolated in a 15-cm-diameter ventilated petri dish and placed in an environmental chamber under its appropriate photoperiod. Females were provided daily with uninfested, greenhouse-grown cotton squares (7–10 mm in diameter at the widest part of the flower bud) with intact bracts until weevil death. This feeding regimen is known to promote a reproductive physiological state (Spurgeon et al. 2003, Spurgeon and Raulston 2006).

Experimental Indices and Their Assessment. Squares were removed daily, and putative feeding (open) and oviposition (sealed) punctures were counted under a dissecting microscope. The total number of punctures in each square was used as a measure of boll weevil puncturing activity according to the method of Everett and Earle (1964). The number of sealed punctures, where a frass plug or waxy substance closed either the puncture or its periphery, was a relative estimate of the number of eggs oviposited (Everett and Ray 1962). An egg–puncture ratio of sealed to total punctures was used to characterize oviposition activity (Everett and Earle 1964). Everett and Ray (1962) indicated that oviposition is adequately estimated by counts of sealed punctures in place of counts of actual eggs. Our laboratory studies indicate a high correlation between egg punctures and actual eggs (unpublished data). We recognize, however, that in other studies, some unsealed punctures contained eggs (Cushman 1911) and that eggs were occasionally deposited on the square surface (Coad 1915, Mayer and Brazzel 1963, Palumbo et al. 1990). Esquivel (2007) indicated that sealed punctures do not necessarily reflect oviposition. Nevertheless, we deemed sealed punctures the best option for indexing egg production, because the alternative, dissection of eggs from the squares, would have precluded subsequent survival estimates.

In addition to monitoring feeding and oviposition, the percentage of eggs that ultimately developed into adult from infested squares, the sex ratio of adult progeny, and development time were estimated from a cohort of squares maintained under each photoperiod. To avoid underestimating the production of adults because of larval cannibalism, only squares containing a single oviposition puncture were selected. The number of oviposition-punctured squares in each cohort varied based on their availability. Totals of 28, 24, 32, 31, and 18 cohorts containing 140, 138, 163, 114, and 98 oviposition-punctured squares were obtained from the photoperiod treatments of 24:0, 14:10, 12:12, 10:14, and 0:24 (L:D) h, respectively. Each cohort was held in a vented 150 by 20-mm plastic petri dish and maintained under the same environmental conditions as the adults. Dishes were observed daily for newly emerged adults beginning on day 10 and continuing to day 20 after oviposition. At day 20, squares were opened to determine whether additional live weevils remained.

Statistical Analyses. A homogeneity of variance test was performed to compare data from both years. Because variances for each dependent variable (i.e., feeding and oviposition punctures) were homogeneous, data from both years were pooled before analysis. Each respective relationship between photoperiod and oviposition punctures, feeding punctures, the ratio of oviposition punctures to total (oviposition + feeding) punctures, and proportion of squares attacked was described by a simple linear regression calculated using PROC GLM (SAS Institute 1999). Data for lifetime oviposition, female adult longevity, total developmental time of progeny (egg to adult emergence), percent emergence, and percentage of progeny that were females were examined by one-way analyses of variance (ANOVA) using PROC GLM (SAS Institute 1999) to determine the influence of photoperiod. When significant F values were obtained, means were separated using the Tukey-Kramer test (TUKEY option of the LSMEANS statement; SAS Institute 1999). Percentage data were analyzed as arcsine square-root-transformed propor-

Table 1. Regression parameters relating photoperiod (PhP) to daily oviposition punctures (OP), daily feeding punctures (FP), ratio of oviposition punctures to total punctures (OP/[OP + FP]), and total squares attacked (SA) by boll weevil females

Relation	n	Slope (SE)	P_{slope}	Intercept (SE)	$P_{intercept}$
PhP–OP	48	0.809 (0.184)	0.001	2.647 (0.604)	0.001
PhP–FP	48	0.619 (0.190)	0.002	3.455 (0.621)	0.001
PhP–OP/[OP + FP]	48	0.027 (0.012)	0.035	0.395 (0.04)	0.001
PhP–SA	48	0.481 (0.107)	0.01	2.025 (0.356)	0.01

tions (Sokal and Rohlf 1995), but results are presented as untransformed means. Survivorships of boll weevils under the different photoperiods were compared using the LIFETEST procedure of SAS (SAS Institute 1999).

An estimate of boll weevil population growth rate was obtained for females corresponding to each photoperiod by calculating life table statistics (Southwood 1966). For each treatment, the jackknife program of Hulting et al. (1990) was used to calculate net reproductive rate (R_o), intrinsic rate of natural increase (r_m), finite capacity of increase (λ, defined as the number of times a population multiplies itself per unit of time), mean generation time (T), doubling time (DT) of the population, and total progeny produced per female.

Results and Discussion

The feeding and oviposition punctures of boll weevil females were significantly affected by photoperiod (Table 1). Boll weevil puncturing activity increased with light exposure from 0 to 24 h. Average egg and feeding punctures, the ratio of oviposition punctures to total punctures, and the percentage of squares attacked each day were greatest when female boll weevils were exposed to the longest photophase (24 and 14 h) and smallest under complete darkness (0-h light). The percentage of days on which females oviposited during their lifetime increased under long photophase ($F = 13.4$, df = 4, $P < 0.01$). On average, females under short photophase oviposited on 69.8 (0-h light) and 68.6% (10-h light) of days during their lifetime, whereas under long photophases of 24, 14, and 12 h, they oviposited on 82.4, 81.2, and 85.2% of days, respectively. The same pattern was observed for the strawberry root weevil, *Otiorhynchus ovatus* L. (Umble and Fisher 2002), and the ladybird *Harmonia axyridis* (Pallas) (Berkvens et al. 2006).

Punctured squares, whether from feeding or oviposition, are aborted by the cotton plant (Fye and Bonham 1970), so rate of attack directly affects yield potential. In the pentatomid *Dichelops melacanthus* Dallas, feeding was continuous at all photophases even though reproductive diapause was induced by short photophase. This type of syndrome, called "oligopause" (Leather et al. 1993), where feeding continues under mild winter conditions even though the adult is in reproductive diapause, is an apt description of the overwintering boll weevil adult that feeds on numerous noncotton plants (Jones and Coppedge 1999, Greenberg et al. 2007a, b, Showler and Abrigo 2007) when temperatures are warm enough for activity and

its reproductive host, cotton, is not available. A higher feeding rate under long photophase than short photophase has been reported for a number of other insects (Niva and Takeda 2003, Omkar and Pathak 2006, Zilahi-Balogh et al. 2006, Doležal and Sehnal 2007). Adult feeding of boll weevils is primarily diurnal (Mally 1901, Wagner et al. 1996), and the positive relationship with photoperiod may simply be the result of more daylight available for foraging (Whittaker and Kirk 2004). Although photoperiod sometimes affects female longevity either positively (Carvalho et al. 2006) or negatively (Ishida et al. 2003, Berkvens et al. 2006), photoperiod did not significantly influence boll weevil adult female longevity (Table 2). Thus, the change in feeding activity was not caused by an associated change in longevity.

Total oviposition punctures, an index of lifetime realized fecundity, was lowest at photoperiods of 0 and 10 h, highest at 12 and 14 h, and intermediate at 24 h of light (Table 2). Like feeding, boll weevil oviposition occurs primarily, although not exclusively, in daylight (Cushman 1911, Mitchell and Cross 1969, Wagner et al. 1996). However, the significant decrease under constant light suggests a signaling function of photoperiod rather than simply increased hours of daylight available for oviposition activity. The same pattern was found for the ladybird, *Coelophora saucia* (Mulsant), where fecundity was highest at 16-h light, lowest at 8-h light, and intermediate at constant light (Omkar and Pathak 2006). Photoperiod sometimes has no effect on fecundity (Aksit et al. 2007, Simelane 2007), but most other reports indicate highest fecundity at long photoperiods (Umble and Fisher 2002, Chocorosqui and Panizzi 2003, Chaisuekul and Riley 2005, Carvalho et al. 2006), even including constant-light treatments (Whittaker and Kirk 2004). In the case of the neuropteran, *Chrysoperla externa* (Hagen), however, fecundity was three-fold greater under an

Table 2. Effects of photoperiod on boll weevil longevity and lifetime oviposition

Photoperiod (L:D) (h)	Longevity (D)	Oviposition punctures
24:0	49.9 ± 7.1a	194.5 ± 28.6b
14:10	42.5 ± 5.7a	251.8 ± 32.4a
12:12	41.8 ± 6.4a	253.4 ± 34.5a
10:14	35.6 ± 5.0a	137.4 ± 19.6c
0:24	33.6 ± 6.3a	127.0 ± 34.1c
	$F = 1.1$; df = 4,45; $P = 0.375$	$F = 4.0$; df = 4,45; $P = 0.008$

Means ± SE within a column followed by different letters are significantly different (Tukey-Kramer).
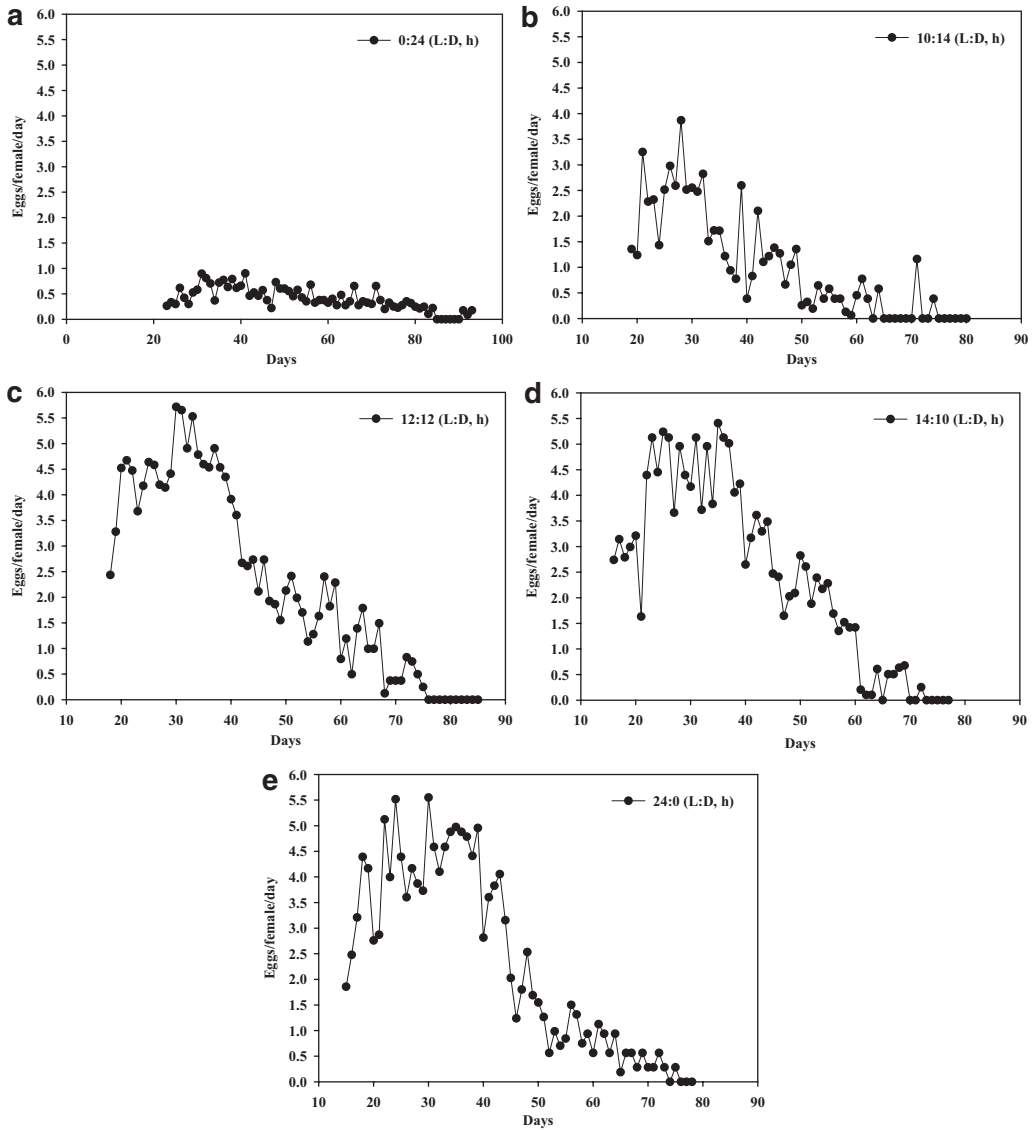
Fig. 1. Lifetime profiles of daily mean oviposition activity of boll weevils in response to different photoperiods: (a) 0:24 (L:D), (b) 10:14, (c) 12:12, (d) 14:10, and (e) 24:0 h.

8-h light photoperiod than under 16-h light (Macedo et al. 2003).

Oviposition punctures increased at a rate of 0.809 per unit (1 h) increase in light exposure. Parallel line analysis showed a similar rate of increase in the feeding and oviposition punctures (Table 1) with light exposure ($F = 1.74$; df = 1,46; $P = 0.26$). A lower increase in the percentage of squares attacked was observed with increasing light exposure; boll weevil females attacked approximately one additional square for each 2-h increase in photophase. Umble and Fisher (2002) determined that strawberry root weevil, *Otiorhynchus ovatus* L., oviposited an average of 15 eggs at 12:12 (L:D) h and an average of 148 eggs at 18:6 (L:D) h. A linear regression model predicted an increase of
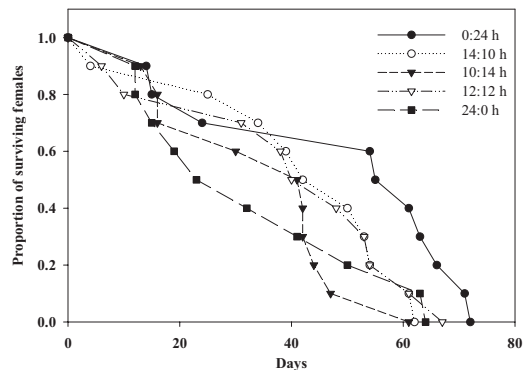

Fig. 2. Survivorship profiles of boll weevil females in response to different photoperiod.

Table 3. Effects of photoperiod on the survival to adulthood, development time, and percent female progeny of boll weevil females

Photoperiod (L:D) (h)	Survival to adulthood (%)	Development time (d)	Females produced (%)
24:0	37.8 ± 3.0b	12.2 ± 0.2d	56.3 ± 4.3a
14:10	51.0 ± 2.2a	11.5 ± 0.2d	50.7 ± 2.8a
12:12	49.4 ± 3.3a	13.6 ± 0.1c	49.7 ± 3.8a
10:14	48.8 ± 4.4a	15.3 ± 0.1b	38.7 ± 5.2b
0:24	18.8 ± 4.0c	19.1 ± 0.8a	17.6 ± 6.1c
	$F = 13.6$; df = 4,128; $P = 0.001$	$F = 86.3$; df = 4,128; $P = 0.001$	$F = 10.8$; df = 4,128; $P = 0.001$

Means ± SE within a column followed by different letters are significantly different (Tukey Kramer).

23 cumulative eggs laid for each 2-h increase of daylength.

Oviposition was significantly influenced by both age (days postconditioning; $F = 15.4$; df = 70,1662; $P = 0.0001$) and photoperiod ($F = 7.1$; df = 4,45; $P = 0.0002$). In addition, the age by photoperiod interaction was significant ($F = 1.7$; df = 252,1662; $P = 0.0001$), indicating that the temporal pattern of oviposition activity differed among females [maintained under different photoperiods (Fig. 1). The oviposition activity curves under the different photoperiod regimes were characterized by a pattern of early increase to a peak, plateau, and decline, but with differences in the timing, magnitude, and duration of these phases (Fig. 1). For females that developed in continuous darkness, oviposition did not begin until 22 d after the conditioning period, after which the average number of oviposition punctures slowly increased to a plateau of 0.5–1.0 eggs/d for ≈80 d, followed by a rapid decline in oviposition (Fig. 1a). Females that developed under 10-h photophase started to oviposit 20 d after conditioning, peaked at 30 d with a lower secondary peak, and plateau at 40 d, followed by an ultimate decline in oviposition (Fig. 1b). For females that developed under photophases of 12, 14, and 24 h, oviposition began earlier, the plateau after peak oviposition was less distinct, and oviposition rates were generally higher than for those developing under short-day photoperiods (Fig. 1c–e).

Boll weevil females that developed under different photoperiod regimens had comparable survivorships (Fig. 2, $\chi^2 = 7.7$, df = 4, $P > 0.1043$). Percent survival from egg to adulthood was lowest for those reared under constant dark, highest (and all similar) under cycling light, and intermediate under constant light (Table 3). The same pattern was observed for a ladybird beetle (Omkar and Pathak 2006). The mechanism

for such an effect is unknown. The negative effect of short photoperiod on longevity was biased against females, resulting in a skewed sex ratio (Table 3). Development time was shortest at 24- and 14-h light and then increased with decreasing light (Table 3); therefore, the decrease in survival to adulthood from 14- to 24-h light cannot be explained by photoperiodic effects on development time. An inverse relationship between immature development rate and length of photophase is common (Chocorosqui and Panizzi 2003, Macedo et al. 2003, Nabeta et al. 2005, Berkvens et al. 2006) but not universal (Niva and Takeda 2003, Omkar and Pathak 2006). Johansson and Rowe (1999) showed that faster development of damselfly nymphs, *Lestes congener* Hagen, under 15-h light photoperiod than under 12-h light was not an artifact of differential nutritional intake associated with more daylight hours for feeding but derived from photoperiod serving as a signal. It is possible that increased developmental rate of boll weevils at longer photoperiods is an artifact, but it is not known if the larvae, which are encased in the cotton square, feed only in daylight.

The values of life table statistics calculated for boll weevil females differed by photoperiod regimens (Table 4). Populations of boll weevils maintained under long photophase are predicted to grow at significantly higher mean constant exponential rates (r_m) than those maintained under short photoperiods (1.8-fold). The net reproductive rate (R_o) was highest at 12- and 14-h light, intermediate at 10- and 24-h light, and very low under constant darkness (Table 4). Similarly, R_o for the ladybird *C. saucia* was highest at 16-h light, intermediate at 24-h light, and lowest at 8-h light (Omkar and Pathak 2006).

The influence of photoperiod on arthropod physiology and activity can potentially enhance or limit the effectiveness of integrated pest management (IPM).

Table 4. Life table statistics of boll weevil females as affected by photoperiod

Photoperiod (L: D) (h)	R_o	r_m	l	T	DT
24:0	39.0 (25.8–52.2)	0.144 (0.13–0.15)	1.154 (1.14–1.17)	25.5 (22.4–28.7)	4.8 (4.5–5.2)
14:10	65.1 (46.2–83.9)	0.147 (0.14–0.16)	1.158 (1.15–1.17)	28.5 (26.4–31.6)	4.7 (4.5–5.1)
12:12	61.5 (42.4–61.5)	0.140 (0.13–0.15)	1.151 (1.14–1.16)	29.4 (27.4–31.4)	4.9 (4.7–5.2)
10:14	25.9 (17.5–34.2)	0.122 (0.11–0.13)	1.129 (1.12–1.14)	26.8 (23.7–29.8)	5.7 (5.2–6.2)
0:24	4.2 (1.6–6.8)	0.038 (0.02–0.05)	1.038 (1.02–1.05)	39.3 (33.7–44.9)	17.7 (10.3–25.4)

Values in parentheses are 95% confidence intervals.

R_o, net reproductive rate; r_m, intrinsic rate of increase; l, finite rate of increase; T, mean period over which progeny are produced (d); DT, doubling time of the population.

We found that feeding, survival, and reproductive rate of the boll weevil increases under long-day photoperiods. Knowledge of the photoperiod-dependent population growth potential provides new insight into boll weevil population dynamics. This can potentially help in designing better sampling protocols and timing insecticide applications, especially as the boll weevil eradication program progressively moves out of temperate regions of the Cotton Belt and into subtropics.

Acknowledgments

References Cited

Aksit, T., I. Cakmak, and G. Ozer. 2007. Effect of temperature and photoperiod on development and fecundity of an acarophagous ladybird beetle, *Stethorus gilvifrons.* Phytoparasitica 35: 357–366.

Berkvens, N., J. Boonte, D. Berkvens, L. Tirry, and P. De Clercq. 2006. Influence of diet and photoperiod on development and reproduction of European populations of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). BioControl 53: 211–221.

Brazzel, J. R., and L. D. Newsom. 1959. Diapause in *Anthonomus grandis* Boh. J. Econ. Entomol. 52: 603–611.

Burke, H. R., W. E. Clark, J. R. Cate, and P. A. Fryxell. 1986. Origin and dispersal of the boll weevil. Bull. Entomol. Soc. Am. 32: 228–238.

Carvalho, A. R., V.H.P. Bueno, E. C. Pedroso, L. I. Kon, A.J.F. Diniz, and R. J. Silva. 2006. Influence of photoperiod on *Orius thyestes* Herring (Hemiptera: Anthocoridae) reproduction and longevity. Neotrop. Entomol. 35: 489–492.

Chaisuekul, C., and D. G. Riley. 2005. Host plant, temperature, and photoperiod effects on ovipositional preference of *Frankliniella occidentalis* and *Frankliniella fusca* (Thysanoptera: Thripidae). J. Econ. Entomol. 98: 2107–2113.

Chocorosqui, V. R., and A. R. Panizzi. 2003. Photoperiod influence on the biology and phenological characteristics of *Dichelops melacanthus* (Dallas, 1851) (Heteroptera: Pentatomidae). Braz. J. Biol. 63: 43–49.

Coad, B. R. 1915. Recent studies of the Mexican cotton boll weevil. U.S. Dep. Agric. Bull. 231: 1–34.

Cushman, R. A. 1911. Studies of the biology of the boll weevil in the Mississippi delta region of Louisiana. J. Econ. Entomol. 4: 432–448.

Denlinger, D. L. 1986. Dormancy in tropical insects. Annu. Rev. Entomol. 31: 239–264.

Doležal, P., and F. Sehnal. 2007. Effects of photoperiod and temperature on the development and diapause of the bark beetle *Ips typographus.* J. Appl. Entomol. 131: 165–173.

Esquivel, J. F. 2007. Evaluation of puncture types as indicators of boll weevil (Coleoptera: Curculionidae) oviposition in cotton squares. Environ. Entomol. 36: 183–186.

Everett, T. R., and J. O. Ray. 1962. The utility of sealed punctures for studying fecundity and egg laying by the boll weevil. J. Econ. Entomol. 55: 634–637.

Everett, T. R., and N. W. Earle. 1964. Boll weevil oviposition responses in cotton squares and various other substrates. J. Econ. Entomol. 57: 651–656.

Fye, R. E., and C. D. Bonham. 1970. Summer temperatures of the soil surface and their effect on survival of boll weevils in fallen cotton squares. J. Econ. Entomol. 63: 1599–1602.

Greenberg, S. M., G. D. Jones, F. Eischen, R. J. Coleman, J. J. Adamczyk, T. X. Liu, and M. Sétamou. 2007a. Survival of boll weevil (Coleoptera: Curculionidae) adults after feeding on pollens from various sources. J. Insect Sci. 14: 503–510.

Greenberg, S. M., T. W. Sappington, M. Sétamou, J. S. Armstrong, R. J. Coleman, and T. X. Liu. 2007b. Reproductive potential of overwintering, F_1, and F_2 female boll weevils (Coleoptera: Curculionidae) in the Lower Rio Grande Valley of Texas. Environ. Entomol. 36: 256–262.

Hulting, F. L., B. Orr, and J. J. Obrycki. 1990. A computer program for calculation and statistical comparison of intrinsic rates of increase and associated life table parameters. Fla. Entomol. 73: 601–612.

Hunter, W. D., and B. R. Coad. 1923. The boll-weevil problem. U.S. Department of Agriculture Farmers' Bulletin 1329. (A1.9, 1329).

Ishida, H., T. Murai, S. Sonoda, H. Yoshida, Y. Izumi, and H. Tsumuki. 2003. Effects of temperature and photoperiod on development and oviposition of *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae). Appl. Entomol. Zool. 38: 65–68.

Johansson, F., and L. Rowe. 1999. Life history and behavioral responses to time constraints in a damselfly. Ecology 80: 1242–1252.

Jones, G. D., and J. R. Coppedge. 1999. Foraging resources of boll weevils (Coleoptera: Curculionidae). J. Econ. Entomol. 92: 860–869.

Leather, S. R., K.F.A. Walters, and J. S. Bale. 1993. The ecology of insect overwintering. Cambridge University Press, Cambridge, United Kingdom.

Lewis, D. K., D. Spurgeon, T. W. Sappington, and L. L. Keeley. 2002. A hexamerin protein, AgSP-1, is associated with diapause in the boll weevil. J. Insect Physiol. 48: 887–901.

Lloyd, E. P., F. C. Tingle, and R. Gast. 1967. Environmental stimuli inducing diapause in the boll weevil. J. Econ. Entomol. 60: 99–102.

Luker, L. A., J. D. Hatle, and S. A. Juliano. 2002. Reproductive responses to photoperiod by a south Florida population of the grasshopper *Romalea microptera* (Orthoptera: Romaleidae). Environ. Entomol. 31: 702–707.

Macedo, L.P.M., B. Souza, C. F. Carvalho, and C. C. Ecole. 2003. Influência do fotoperíodo no desenvolvimento e na reprodução de *Chrysoperla externa* (Hagen) (Neuroptera: Chrysopidae). Neotrop. Entomol. 32: 91–96.

Mally, F. W. 1901. The Mexican boll weevil. U.S. Department of Agriculture Farmers' Bull. 130.

Mangum, C. L., N. W. Earle, and L. D. Newsom. 1968. Photoperiodic induction of diapause in the boll weevil, *Anthonomus grandis.* Ann. Entomol. Soc. Am. 61: 1125–1128.

Mayer, M. S., and J. R. Brazzel. 1963. The mating behavior of the boll weevil, *Anthonomus grandis.* J. Econ. Entomol. 56: 605–609.

Mitchell, H. C., and W. H. Cross. 1969. Oviposition by the boll weevil in the field. J. Econ. Entomol. 62: 604–605.

Nabeta, F. H., M. Nakai, and Y. Kunimi. 2005. Effects of temperature and photoperiod on the development and reproduction of *Adoxophyes honmai* (Lepidoptera: Tortricidae). Appl. Entomol. Zool. 40: 231–238.

Niva, C. C., and M. Takeda. 2003. Effects of photoperiod, temperature and melatonin on nymphal development, polyphenism and reproduction in *Halyomorpha halys* (Heteroptera: pentatomidae). Zool. Sci. 20: 963–970.

Omkar, and S. Pathak. 2006. Effects of different photoperiods and wavelengths of light on the life-history traits of an aphidophagous ladybird, *Coelophora saucia* (Mulsant). J. Appl. Entomol. 130: 45–50.

Palumbo, J. C., T. F. Watson, and D. K. Bergman. 1990. Globemallow, Sphaeralcea spp., as reproductive host for the boll weevil (Coleoptera: Curculionidae) in Arizona. J. Econ. Entomol. 83: 392–397.

Sappington, T. W., and D. W. Spurgeon. 2000. Preferred technique for adult sex determination of the boll weevil (Coleoptera: Curculionidae). Ann. Entomol. Soc. Am. 93: 610–615.

SAS Institute. 1999. SAS/STAT user's guide, release 8.01 ed. SAS Institute, Cary, NC.

Showler, A. T., and V. Abrigo. 2007. Common subtropical and tropical nonpollen food sources of the boll weevil (Coleoptera: Curculionidae). Environ. Entomol. 36: 99–104.

Simelane, D. O. 2007. Influence of temperature, photoperiod and humidity on oviposition and egg hatch of the root-feeding flea beetle *Longitarsus bethae* (Chrysomelidae: Alticinae), a natural enemy of the weed *Lantana camara* (Verbenaceae). Bull. Entomol. Res. 97: 111–116.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry. The principles and practice of statistics in biological research, 3rd ed.W. H. Freeman and Co., New York.

Southwood, T.R.E. 1966. Ecological methods: with particular reference to the study of insect populations. Kluwer, Dordrecht, The Netherlands.

Spurgeon, D. W., and J. R. Raulston. 1998. Diapause induction in subtropical boll weevils, pp. 1019–1026. *In* P. Dugger and D. Richter (eds.), Proceeding of the Beltwide Cotton Conference, National Cotton Council, Memphis, TN.

Spurgeon, D. W., T. W. Sappington, and C. P.-C. Suh. 2003. A system for characterizing reproductive and diapause morphology in the boll weevil (Coleoptera: Curculionidae). Ann. Entomol. Soc. Am. 96: 1–11.

Spurgeon, D. W., and J. R. Raulston. 2006. Boll weevil (Coleoptera: Curculionidae) adult diapause responses to selected environmental and dietary conditions. Ann. Entomol. Soc. Am. 99: 1085–1100.

Umble, J. R., and J. R. Fisher. 2002. Influence of temperature and photoperiod on preoviposition duration and oviposition of *Otiorhynchus ovatus* (Coleoptera: Curculionidae). Ann. Entomol. Soc. Am. 95: 231–235.

Wagner, T. L., R. L. Olson, J. L. Willers, and M. R. Williams. 1996. Modeling and computerized decision aids, pp. 206–249. *In* E. G. King, J. R. Phillips, and R. J. Coleman (eds.), Cotton insects and mites: characterization and management. Cotton Foundation Reference Book Series, No. 3. The Cotton Foundation Publisher, Memphis, TN.

Wagner, T. L., E. J. Villavaso, and J. L. Willers. 1999. Diapause in the boll weevil (Coleoptera: Curculionidae): life-stage sensitivity to environmental cues. Ann. Entomol. Soc. Am. 92: 396–402.

Whittaker, M. S., and W.D.J. Kirk. 2004. The effect of photoperiod on walking, feeding, and oviposition in the western flower thrips. Entomol. Exp. Appl. 111: 209–214.

Zilahi-Balogh, G.M.G., J. L. Shipp, C. Cloutier, and J. Brodeur. 2006. Influence of light intensity, photoperiod, and temperature on the efficacy of two aphelinid parasitoids of the greenhouse whitefly. Environ. Entomol. 35: 581–589.